## AN ADDITIONAL STUDY ON THE NESTING BEHAVIORS OF SPECIES OF *MISCOPHUS* (HYMENOPTERA: SPHECIDAE)

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Abstract.-Additional observations made on nesting females of Miscophus (Miscophus) americanus Fox, M. (Nitelopterus) slossonae barberi (Krombein), and M. (Nitelopterus) s. slossonae (Ashmead) in New York and Florida extend the range in variation in their ecologies and nesting behaviors. Miscophus americanus females nested in sand cliffs, left entrances open and oriented and brought prev to the nests in flight. Their nests were short and simple and were stored with 3-14 tiny, mostly Theridion spp. (Theridiidae). Miscophus slossonae barberi nested in flat sand, usually left entrances open and oriented by running around the entrances, and transported prey on the ground or in short, low flights. Their longer, simple nests were stocked with 5-14 tiny lycosids and salticids. Miscophus s. slossonae constructed the longest and deepest nests of the three taxa, and stored 7-8 tiny spiders of a variety of families (Theridiidae, Micryphantidae, Oxyopidae, Lycosidae, Gnaphosidae, Salticidae). This subspecies nested in flat sand, closed nest entrances or left them open during provisioning, oriented in flight or on the ground, transported prey in low, short flights or on the ground, and often took longer than a day to complete a nest.

In 1969 I summarized much of the known biological and behavioral information for the Nearctic and exotic *Miscophus*, including species in the subgenera *Miscophus* and *Nitelopterus*. Bohart and Menke (1976) encapsuled this information in three paragraphs, and Krombein (1979) summarized the known ecological data, prey records, and biological references for species of *Miscophus*. Neither compilation added much new information to the existing pool of data on the nesting behaviors of species of *Miscophus* simply because no studies of species in this genus were published during the 1970's except for a note on *Nitelopterus* (=*Miscophus*) evansi Krombein by Evans (1970). The intent of the present paper is to provide new information on species in both Nearctic subgenera in order to extend the range of biological knowledge for this little-studied group of wasps.

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The species of *Miscophus* which are treated in this paper, their localities, dates of observation and collection, and associated ethological note numbers are as follows: *M.* (*Miscophus*) americanus Fox—Selkirk Shores St. Pk., Oswego Co., N.Y., 14 June 1971–22 August 1972 (MI 3-6, 8-13); Arcadia, DeSoto Co., Fla., 27 March 1972 (MI-7); *M.* (*Nitelopterus*) slossonae barberi (Krombein)—Archbold Biol. Sta., L. Placid, Highlands Co., Fla., 15 March–6 April 1973 (NI-21-24); *M.* (*Nitelopterus*) s. slossonae (Ashmead)—Arcadia, DeSoto Co., Fla., 8 April 1971–28 March 1973 (NI-17-20, 25). The wasps and prey have been deposited in the insect and invertebrate collections of the S.U.N.Y. College of Environmental Science and Forestry, Syracuse.

### Miscophus (Miscophus) americanus Fox

Eleven nests were constructed into vertical sand cliffs. The nest at Arcadia, Fla., was situated halfway up a 2.4 m steep cliff, whereas the 10 nests at Selkirk Shores St. Pk., N.Y., were located from 18 to 76 ( $\bar{x}$ , 53) cm from the top of a 1.8 m high cliff. Although I was unable to locate their nests, provisioning females of *M. americanus* were seen flying to and from a 1 m high sand cliff near the entrance to Presque Isle St. Pk., Erie Co., Pa., during 4–9 July 1971.

Several females began nests in shallow pre-existing depressions in the cliff face or beneath overhanging rootlets in concealed situations. Two such nest entrances were only 1 cm apart, although the cells of these respective nests were separated by 3 cm.

Burrow construction components conformed to those described by Kurczewski (1969), although false starts were made less frequently when nesting in sand cliffs than when nesting in flat sand. The duration of burrow construction for four females averaged 35 (21–44) minutes.

All prey (32) of females of *M. americanus* brought to the nest were carried in flight. Nesting in sand cliffs may restrict females to practice this method of transport. Size of prey influenced the speed of flight but not type of transport. The mechanisms of prey carriage were similar to those described by Kurczewski (1969).

The period of time between 13 consecutive provisioning trips of two females averaged 10 (2–29) minutes. Neither size of prey nor position within the sequence influenced the period of time between such trips. Seven larger prey were taken into the open entrances, released 1–2 mm inside the burrows, and pulled in from inside after the wasps had turned around, whereas 11 smaller prey were transported directly into open burrows without females releasing the spiders. One female exited in flight from 3 to 30 ( $\bar{x}$ , 8.4; N = 10) seconds after entering with prey. The time between consecutive exits decreased steadily from 1130 hours (30 seconds) to 1326–1334 hours (3 sec-

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onds), perhaps a reflection of increased familiarity with the burrow confines and/or increased sand surface temperature.

Upon taking the last prey into the nest females of *M. americanus* briefly appeared headfirst inside the entrance, turned around, and reentered the burrow. From 5 to 9 minutes later they were observed in their entrances making nest closures. Details of the closure were as described by Kurczewski (1969), except for extensive use of the mandibles to break down sand from the walls of the burrows. Five closures were completed by females between 1315 and 1605 hours. They averaged 9.9 (8–15) minutes in duration. This closure activity culminated in burrows filled with loose sand for much of their lengths from the fully provisioned cells to within 1–5 mm of the entrances.

Ten nests of *M. americanus* were short, simple (spurless) and unicellular. Four nests exhibited some lateral curvature upon entering the cliff face, whereas six went in rather straight. The burrows coursed inward almost horizontally with most declining from 5 to 15° with the horizon. Nest entrances were 2.5–3.0 mm in diameter and the burrows, 2.0–2.5 mm. Burrow lengths ranged from 2.0 to 3.8 ( $\bar{x}$ , 2.8) cm, including cell length. The ellipsoid-shaped cells were 4–6 mm wide, 4–6 mm high and 6–12 mm long.

Females of *M. americanus* preyed almost totally on spiders of the family Theridiidae as follows: *Theridion differens* Emerton, 18 ad.  $\Im$ , 1 pen.  $\Im$ ; 19 imm.; *T. flavonotatum* Becker, 2 ad.  $\Im$ ; *T. murarium* Emerton, 22 imm.; *T. redimitum* (Linn.), 1 imm.; and, *T.* sp., 5 imm. In Florida one wasp provisioned partly with four immature *Araneus* sp. (Araneidae), an exceptional record. Many of the prey were moving the legs and extruding silk from the spinnerets.

Nine fully provisioned cells of *M. americanus* contained from 3 to 14 ( $\bar{x}$ , 7.7) prey per cell. The individual spiders ranged in weight from 0.5 to 5.9 ( $\bar{x}$ , 1.9; N = 67) mg. Four captor wasps averaged 4.4 (3.0–5.7) mg in weight. The contents of eight fully provisioned cells ranged in weight from 8.0 to 20.0 ( $\bar{x}$ , 14.7) mg.

The prey of *M. americanus* were placed variously in the cells as follows: ventral side upward, head inward, 15; dorsal side upward, head inward, 26; dorsal side upward, head outward, 13; sideways, head upward or downward, 8. No prey were placed ventral side upward and head outward. There was no particular pattern as to the exact positioning of these spiders within the cell, i.e., individuals positioned dorsal side upward and head inward were found at the back or front ends of the cell or toward the center.

The egg of *M. americanus* was attached to the spider as described and figured by Kurczewski (1969). Eggs measured  $1.25-1.50 \times 0.40-0.45$  mm. In eight cells four eggs were attached to the base of the left side of the spider's abdomen and four to the base of the right side. The egg-bearing

spiders were placed in the cells either dorsal side upward and head inward (6) or dorsal side upward and head outward (2). They were positioned in the cells near the back (3), middle (2), or front end (3). Spiders with eggs weighed 1.8-5.9 ( $\bar{x}$ , 3.2) mg and were the largest (3), second largest (3), third largest (1), or second smallest (1) individuals in the cells. In one cell there was an egg of the same size and shape as that of *M. americanus* on the floor in addition to the egg attached to the spider!

### Miscophus (Nitelopterus) slossonae barberi Krombein

Three nests were excavated and examined in flat, bare, white sand at the Archbold Biological Station. Several other females were observed nesting in flat or sloping, bare, white sand near Lakes Annie and Placid, Highlands Co., Fla., during March and April 1973, but data were not gathered on these individuals.

Females searching for nesting sites made numerous false starts, especially in the morning between 1100 and 1200 hours (E.S.T.). Components of burrow construction were similar to those described by Krombein and Kurczewski (1963) and Kurczewski (1969). One wasp started a burrow in a depression in bare sand and completed it 1 hour and 58 minutes later. Females completing burrows exited headfirst, turned 180°, walked back and forth on or around the tumulus, entered and exited from the burrow from one to four times, and then began walking increasingly farther away from the entrance in circular or zig-zag routes, an apparent form of orientation. These movements increased in rapidity until the females flew off to hunt.

Prey transport involved a female grasping the spider with the mandibles by its forelegs or pedipalps, head forward and ventral side upward, and walking rapidly forward on the ground or making short, "hopping" flights using the wings. Several prey were released and abandoned when the provisioning wasps were attacked by foraging ants. Such females returned to their nests and immediately closed the nest entrances with sand. Some wasps periodically returned to their nests without prey, examined the open entrance and flew off or entered the burrow, exited several seconds later and flew away.

The size of prey influenced the manner in which the provisioning wasp entered her open nest. Females with 16 "smaller" prey went directly into their open nests without releasing the spiders, whereas wasps with 9 "larger" prey released the spiders just inside the entrances, went into the burrows, turned around and pulled the prey inside. Such wasps spent an average of 19 (5-42; N = 15) minutes between consecutive prey. These females reappeared in their entrances from 10 to 180 ( $\bar{x}$ , 49; N = 14) seconds after placing their prey in the nests. The longest periods of time were recorded near the end of the provisioning sequence.

Components of final closing the nest were essentially identical to those

described for the nominate subspecies by Kurczewski (1969). Three final closures averaged 38 (27–46) minutes in duration. Closed nests contained burrows completely filled with sand. One female attempted to bring prey into a burrow that had been filled with sand and contained prey with one of the spiders bearing a wasp's egg!

The three nests of *M. slossonae barberi* contained straight or slightly curved burrows with diameters of 2 mm and ended in single cells. These burrows ranged from 4.9 to 6.1 ( $\bar{x}$ , 5.3) cm in length and from 2.9 to 3.9 ( $\bar{x}$ , 3.5) cm in depth, including cell length and height, respectively. The cells averaged 3.5 (3–4) mm high, 3.5 (3–4) mm wide and 5.5 (5–6) mm long. The diameter of the burrow entrance in all three nests was 2.5 mm.

The females preyed upon tiny wolf and jumping spiders as follows: LY-COSIDAE: *Pirata* sp., 1 imm.; *Schizocosa* sp., 1 imm. SALTICIDAE: *Habrocestum* sp. nr. *pulex* (Hentz), 2 ad.  $\Im$ , 6 ad.  $\eth$ , 1 imm.  $\eth$ , 15 imm. The spiders were incompletely paralyzed, moved their legs, and extruded silk from the spinnerets.

The three fully provisioned cells contained from 5 to 14 ( $\bar{x}$ , 8.3) prey per cell. The spider individuals ranged in weight from 0.2 to 2.8 ( $\bar{x}$ , 1.2; N = 26) mg. One wasp weighed 2.2 mg. The cell contents ranged in weight from 4.3 to 15.4 ( $\bar{x}$ , 9.2) mg.

The prey of *M. slossonae barberi* were placed in various positions within the cells as follows: ventral side upward, head inward, 9: dorsal side upward, head inward, 11; dorsal side upward, head outward, 3; and, sideways, head upward or downward, 2. None of the prey were positioned ventral side upward and head outward.

The egg of this subspecies was affixed to the spider's abdomen as indicated and figured for *M. americanus* by Kurczewski (1969). Eggs measured from 1.2 to 1.8 mm in length. All three eggs were affixed to the left sides of the spiders' abdomens and the three spiders with eggs were positioned dorsal side upward and head inward in the cells. The three spiders were located at the front or back end or in the middle of the cell. Egg-bearing spiders weighed from 1.4 to 2.2 ( $\bar{x}$ , 1.9) mg. They were the largest prey in each of the three cells.

### Miscophus (Nitelopterus) s. slossonae (Ashmead)

Four nests were constructed into the white sand flats bordering the Peace River, west of Arcadia, Fla. One nest was dug into the slope of an ant-lion pit, near the top, another was concealed beneath two overhanging grass blades, a third into the edge of a cow's hoofprint, and a fourth beneath an overhanging *Mimosa* plant. A fifth wasp attempted to dig in a depression caused by a marking stake. Only one female attempted to nest in bare sand, devoid of vegetation or depressions.

Burrow construction components were identical to those described by

Kurczewski (1969). One wasp searched for only 10 minutes before remaining in one place and completing her burrow. She took 50 minutes to completion, beginning at 1159 and ending at 1249 hours (E.S.T.). She removed sand from the burrow to a distance of 20 mm from the entrance. The resulting tumulus was elongate-ovoidal in shape.

One wasp made a 2-second-long temporary closure of the nest entrance after completing the burrow, after which the entrance remained one-third open at the top. She then ran around the area of the entrance for 30 seconds and flew away. This female returned from her hunting excursions several times but never entered the burrow. Two other females made no closures of their entrances while obtaining a total of six prey. Another wasp, however, after leaving the nest open during her first two provisioning trips made a complete closure of the nest entrance as she obtained her third prey. After placing the spider inside, she exited and closed the entrance with sand. The duration of this closure was 25 seconds; she periodically interrupted five times to turn toward the entrance. This was followed by an orientation flight.

Another wasp opened her nest and entered at 1012 hours (E.S.T.), after spending the night in a short burrow 50 cm away. She exited, turned and entered her nest twice more, then made an 18-second-long temporary closure, including two turns toward the entrance. She, too, made an orientation flight following the closure. The female returned both without and with prey between 1042 and 1052 hours, each time closing the entrance with sand upon leaving. She brought two prey to the nest at 1101 and 1114 hours but did not close the entrance with sand upon leaving. The female made no other closures of this nest until she finally closed it after ovipositing at 1201 hours.

Other females observed later in the day (1400–1530 hours) made brief temporary closures of their nest entrances, which included turning toward the entrance one or more times, and culminated in low orientation flights, or, they left the nest entrance open between consecutive provisions and oriented by running around the entrance on the sand. In two cases females hunted spiders on the sand near their nest entrances. One wasp stung a small spider only 1.5 m from her entrance. Subsequent prey were captured even closer to the entrance in all directions of the compass.

Details of prey transport for this subspecies were described by Krombein (1964) and Kurczewski (1969). Smaller wasps with black and red abdomens brought prey on the ground, whereas one noticeably larger provisioning female with a mostly all-red abdomen made 30-cm-long flights. Females spent from 5 to 44 ( $\bar{x}$ , 16; N = 9) minutes between consecutive prey. Neither size of prey nor position within the provisioning sequence influenced the period of time between consecutive trips. Two larger prey were released inside the entrances by females and pulled in from inside the burrow, after

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the wasps had turned around. Eight smaller spiders were taken into the nests without being released or were released and taken in as described above. In the latter case most such releases were determined by a temporary closure of the nest entrance in which case the wasp had to relinquish the spider in order to remove the sand fill. But one release occurred with an open entrance prior to making the final nest closure.

Females of M. s. slossonae exited from 15 seconds to 3.5 minutes (N = 7) later. In the case of the wasp spending a long period of time inside the nest prior to exiting, such entries had been deterred by a sand-filled entrance, i.e., temporary closure. One female twice removed her nest closure without relinquishing the spider, i.e., she held the spider with the middle legs as she removed the sand fill with the forelegs.

Another wasp began her final closure after entering her open nest with prey at 1159 hours. The components were identical to those described for this subspecies by Kurczewski (1969). She completed filling the burrow and distributing sand on the area of the entrance at 1216, taking a total of 17 minutes for the closure. Females that did not begin and complete nests in a single day closed their burrow entrances completely with sand in late afternoon, returning often after several minute intervals to throw additional sand on the fill. They then moved 0.5–1.0 m away and dug short burrows in which they spent the night, facing head outward. Females emerged head first from these resting burrows usually between 0930 and 1030 hours (E.S.T.) and completed provisioning their nests after opening the entrances.

Nests of *M. s. slossonae* were moderately short, shallow and unicellular. Nests were either straight or curved considerably. Nest entrances and burrows were 1.5-2.0 mm in diameter. Four burrows averaged 7.8 (7.4–8.4) cm in length and 5.6 (4.9–6.0) cm in depth, including cell length and height. The elongate-ovoidal cells were 3.5-4.0 cm wide and 6-7 mm long.

Females of this subspecies preyed upon a variety of small spiders as follows: THERIDIIDAE: Steatoda fulva (Keys.), 1 imm.  $\delta$ . MICRYPHAN-TIDAE: Grammonata sp. nr. texana Banks, 1 ad.  $\mathfrak{P}$ ; Grammonata sp., 5 imm. OXYOPIDAE: Oxyopes salticus Hentz, 1 imm. LYCOSIDAE: Pirata sp., 1 imm.; Arctosa littoralis (Hentz), 1 imm. GNAPHOSIDAE: Micaria sp., 1 imm.  $\delta$ . SALTICIDAE: Pellenes sp., 7 imm. Prey were incompletely paralyzed and moved their legs and emitted silk from the spinnerets.

Two completely provisioned nests contained 7 and 8 prey. Two unfinished nests held 5 and 2 spiders. Individual spiders weighed from 0.5 to 3.5 ( $\bar{x}$ , 1.3; N = 22) mg. Two wasps weighed 1.5 and 2.0 mg. The contents of two fully provisioned cells weighed 9.0 and 11.5 mg.

Prey of M. s. slossonae were placed variously in the cells as follows: ventral side upward, head inward, 8; dorsal side upward, head inward, 11; and, dorsal side upward, head outward, 3. No prey were placed ventral side upward and head outward or sideways. The contents of one cell with 7 prey

exemplifies the heterogeneity of the prey positioning: 2, dorsal side upward, head outward at the back end; 3, dorsal side upward, head inward in the middle; and, 2, ventral side upward, head inward at the front end.

Eggs of *M. s. slossonae* were attached to the spiders as described and figured for *M. americanus* by Kurczewski (1969). Eggs ranged from 1.0 to 1.5 mm in length. Two eggs were affixed to the bases of the left sides of the spiders' abdomens. These prey were placed dorsal side upward and head inward in the middle of the cells. Spiders bearing eggs weighed 1.0 and 1.5 mg: these prey were the second largest individuals in the cells, in each case an imm. *Pellenes* sp.

### DISCUSSION

*Miscophus* (*Miscophus*) americanus, *M*. (*Nitelopterus*) slossonae barberi, and *M*. (*Nitelopterus*) s. slossonae are multivoltine throughout much of their range. Even in upstate New York, *M. americanus* nests from mid-June through September. All species inhabit areas of sandy soil with sparse vegetation, preferring to build burrows in pits, depressions and hoof- and footprints. The nests observed in the present study were constructed from the sand surface. Whereas both subspecies of *M.* (*Nitelopterus*) slossonae preferred to nest in flat sand, *M.* (*Miscophus*) americanus dug nests into vertical sand cliffs. This is in sharp contrast with my earlier (1969) paper in which I reported *M. americanus* nesting in flat or slightly sloping sandy soils in New York and Florida.

The behavioral components involved in digging the burrows are similar for all species. Soil removal is accompanied by little or no leveling of the tumulus in front of the entrance. Females of M. (*Miscophus*) americanus spent less time during burrow construction than either subspecies of M. (*Nitelopterus*) slossonae, probably a reflection of the shorter burrows of the former species.

Upon completion of the burrow females of *M*. (*Miscophus*) americanus and *M*. (*Nitelopterus*) slossonae barberi left the nest entrance open as they went in search of prey. Some females of *M*. (*Nitelopterus*) s. slossonae left entrances open whereas other females, especially those nesting in late morning, made brief sand closures of their entrances prior to hunting. Both subspecies of *M*. (*Nitelopterus*) slossonae were observed making nest closures during the provisioning sequence, typical slossonae more frequently and under more varied conditions than slossonae barberi. Closures made by the latter subspecies were observed during periods of ant interference. The extent of temporary closure and the situations surrounding its presence or absence have been discussed in some detail by Krombein and Kurczewski (1963) and Kurczewski (1969), suffice it to say it is an extremely variable behavior.

Females of M. (Miscophus) americanus and both subspecies of M. (Ni-

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telopterus) slossonae were observed making orientation flights or orientation "runs" or "walks" following burrow construction and exit from the entrance. Orientation flights predominated in the case of *M. americanus* females nesting in sand cliffs, whereas those females nesting in flat or slightly sloping sand in an earlier study (Kurczewski, 1969) oriented predominantly by running or walking around the entrance. In *M. slossonae*, especially *s. slossonae*, females which made temporary nest closures usually oriented by flying, whereas those which left nest entrances open oriented by running around the entrances. In neither *M. s. slossonae* nor *M. slossonae barberi* was there a correlation between the form of orientation and the manner in which the prey was brought to the nest. *Miscophus americanus* females, which often oriented in flight in front of sand cliffs, brought prey to their nests in flight.

Females of *M*. (*Nitelopterus*) *s. slossonae* hunted and captured prey near their nest entrances, whereas those of *M*. (*Miscophus*) americanus often flew rather long distances in order to obtain prey. The former species preyed upon either wandering or web-spinning spiders on or near the sand surface which were transported to the nest mostly on the ground, whereas *M*. americanus females took mostly combfooted spiders from webs above ground and brought these prey to their nests in flight. In at least *M*. (*Nitelopterus*) *s. slossonae* the prey is stung and paralyzed incompletely. Incomplete paralysis of the prey involving spiders moving their legs and emitting silk from the spinnerets was the rule also in *M. slossonae barberi* and *M. (Miscophus) americanus*. In contrast to earlier studies of species in this genus (Cazier and Mortenson, 1965; Krombein and Evans, 1954; Krombein and Kurczewski, 1963), I found no evidence of amputation of the legs of the prey in the present study.

The mechanisms of prey transport among species in this genus have been summarized by Kurczewski (1969). The exact manner of transport and the extent of the flight varies with the species of wasp and the relative sizes of the females and their prey. *Miscophus* (*Nitelopterus*) s. slossonae, for example, practiced ground transport as well as carrying prey in short flights, whereas *M*. (*Miscophus*) americanus invariably transported prey in long, extensive flights. Both Kurczewski (1969) and Bohart and Menke (1976) have speculated on the relationship between the method of prey transport and the length of wings and degree of wing venation in some of the species.

In the species of *Miscophus* studied herein the manner in which prey was taken into the nest was dependent upon the absence or presence of a temporary closure and size of spider. Smaller spiders were usually taken directly into the open burrow, whereas larger prey were often released temporarily just outside or inside the entrance and pulled in from inside after the wasp had turned around.

The behavioral components involved in final closing the nests are similar

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Species of Prey	No. Specimens, Stage	Source
Miscoph	us (Miscophus) american	us
THERIDIIDAE		
Theridion australe Banks	5 imm.	Kurczewski, 1969
Theridion differens Emerton	18 ad. ♀; I pen. ♂; 37 imm.	Kurczewski, 1969; MI-3-6, 8-13
Theridion flavonotatum Becker	2 ad. 9	MI-7
Theridion murarium Emerton	24 imm.	Kurczewski, 1969; MI-3, 4 6, 8, 9, 11, 13
Theridion redimitum (Linn.)	1 imm.	MI-3
Theridion sp.	5 imm.	M1-7
ARANEIDAE		
Araneus sp.	4 imm.	MI-7
Miscophus (	Nitelopterus) slossonae b	arberi
LINYPHIIDAE		
Meioneta formica (Emerton)	1 ad. 9	Krombein and Kurczewski, 1963
LYCOSIDAE		
Pirata sp.	1 imm.	NI-24
Geolycosa sp.	Limm.	Krombein, 1964
Schizocosa sp.	Limm.	NI-22
Lycosa sp.	1 imm.	Krombein, 1964
SALTICIDAE		
Habrocestum sp. nr. pulex (Hentz)	2 ad. ♀; 6 ad. ♂; 1 imm. ♂; 15 imm.	N1-21-24
Pellenes sp.	1 imm.	Krombein and Kurczewski, 1963
Miscophu	s (Nitelopterus) s. slossor	nae
THERIDIIDAE		
Steatoda erigoniformis (Cambridge)	10 imm.	Kurczewski, 1969
Steatoda fulva (Keys.)	l imm. ð	NI-17
MICRYPHANTIDAE		
Grammonata sp. nr. texana Banks	1 ad. ♀	NI-18
Grammonata sp.	5 imm.	NI-17-19
LINYPHIIDAE		
Meioneta formica (Emerton)	۱ad. ۹	Krombein and Kurczewski, 1963

Table 1. Species of prey of some species of Miscophus.

Table I. Continued.

Species of Prey	No. Specimens, Stage	Source
TETRAGNATHIDAE		
Tetragnatha laboriosa Hentz	4 imm.	Kurczewski, 1969
OXYOPIDAE		
Oxyopes salticus Hentz	Limm.	NI-18
LYCOSIDAE		
Pirata sp.	1 imm.	NI-17
Pardosa sp.	1 imm.	Kurczewski, 1969
Arctosa littoralis (Hentz)	1 imm.	N1-20
Arciosa sp.	1 imm.	Krombein and Kurczewski, 1963
Lycosa sp.	4 imm.	Krombein and Kurczewski, 1963: Krombein, 1964
GNAPHOSIDAE		
Micaria sp.	1 imm. ð	N1-20
SALTICIDAE		
Habrocestum pulex (Hentz)	1 imm.	Krombein and Evans, 1955
Metaphidippus galathea (Walck.)	l imm.	Krombein and Evans, 1954
Metaphidippus sp.	1 imm.	Krombein, 1964
Pellenes sp.	7 imm.	NI-18, 19
DICTYNIDAE		
Dictyna altamira Gertsch and Davis	1 ad. 9	Krombein and Kurczewski. 1963

in not only the species studied herein but also in many other species in both subgenera. The typical closing components in their exact sequence have been detailed by Kurczewski (1969).

The nests of most species of *Miscophus* are relatively short, shallow and unicellular, the exception being *M. evansi* (Evans, 1963, 1970) and some exotic species. Although data on nest dimensions, as summarized by Kurczewski (1969), indicated that the nests of *M. (Miscophus) americanus* and the two subspecies of *M. (Nitelopterus) slossonae* are similar, an analysis of the burrow lengths (and cell depths in *M. slossonae*) in the present study revealed that nests of *M. (Nitelopterus) s. slossonae* are longer and deeper than those of *M. (Nitelopterus) slossonae* barberi and about twice as long as those of *M. (Miscophus) americanus*. The differences between the nest dimensions of these species clearly reflect differences in the habitats in which they nested. Cells of *M. americanus* were longer, wider and higher

than those of either subspecies of *M. slossonae* and prey biomass was usually greater.

Kurczewski (1969) summarized the prey specificity or lack thereof of species in the subgenera Miscophus and Nitelopterus. Most of the species appear to restrict their hunting activities to specific ecological situations where particular kinds of prey occur. Thus, M. (Miscophus) americanus preyed almost entirely upon combfooted web-spinning spiders belonging to the family Theridiidae (Table 1). The record of this species using immature araneids in Florida is exceptional, although females of M. americanus accepted anesthetized immatures of Eustala (Araneidae) when they were substituted at the nest entrance for prey theridiids (Kurczewski, 1969). Both subspecies of M. (Nitelopterus) slossonae were more general in their selection of prey. Miscophus slossonae barberi preved upon small, immature Lycosidae and Salticidae (Table 1). One record of Meioneta formica (Linvphiidae) for this subspecies was exceptional (Krombein and Kurczewski, 1963). Thus, this subspecies of M. slossonae captures mostly wandering spiders on or near the sand surface. Miscophus s. slossonae is heterogeneous in its selection of prey, taking no less than nine families of spiders from a variety of ecological situations (Table 1). Underscoring this lack of specificity is the fact that members of the Theridiidae, Micryphantidae, Linyphiidae, Tetragnathidae and Dictynidae are web-spinners, whereas those of the Oxyopidae, Lycosidae, Gnaphosidae and Salticidae are wanderers.

The number of prey stored in the fully provisioned cells of the species of *Miscophus* does not vary inversely with the sizes of the prey, as indicated by Kurczewski (1969). This is substantiated by the diversity in the biomass as evidenced by the total weights of the prey contents, e.g., *M. americanus* (8–20 mg). Some of the fully provisioned cells of this species and of *M. slossonae barberi* contained much empty space whereas others were fully packed with prey. Variable weather conditions and/or prey abundance may influence the number of prey stored in the cells.

The prey of *M*. (*Miscophus*) americanus and both subspecies of *M*. (*Nitelopterus*) slossonae were placed in the cell variously with a preponderance of spiders positioned dorsal side upward and head inward (48), then ventral side upward and head inward (32) and dorsal side upward and head outward (19). No prey were positioned ventral side upward and head outward. Egg-bearing prey of these species were positioned either dorsal side upward and head inward (2). The dorsal side upward positioning of the egg-bearing spider is related to the affixment of the egg, i.e., laterally on one side or the other to the base of the spider's abdomen (see Fig. 5, Kurczewski, 1969). The egg may extend well beyond the spider's dorsal abdominal terga and would become dislodged if the prey were placed ventral side upward on the floor of the cell. Egg-bearing spiders were placed in the cells either at the front (4) or back (4) ends or toward the middle (4), with no set pattern for either *M*. ameri-

*canus* or either subspecies of *M. slossonae*. This find is in agreement with previous studies on these species and *M. kansensis* (Kurczewski, 1969). Spiders with eggs were frequently larger than other prey in the cells or of the same size. Whereas the mean weights of prey for *M. americanus*, *M. slossonae barberi*, and *M. s. slossonae* were 1.9, 1.2, and 1.3 mg, those for egg-bearing prey of these species were 3.2, 1.9, and 1.3 mg, respectively.

Some unusual ovipositional behaviors were noted in the present study. One cell of *M*. *americanus* contained two eggs of the same size and shape. one affixed to the prey in the position typical of the genus and the other lying on the floor of the cell. It is possible that one egg was dislodged from a spider during oviposition, inducing the female to oviposit again on the same or another prev; or, a second wasp may have inadvertently entered the wrong nest and oviposited and this egg was dislodged by the resident female as she laid her egg. Despite the fact that Kurczewski (1969) stated that the egg of species of *Miscophus* is not deposited until the full complement of prey has been placed in the cell, the possibility of rare instances of progressive provisioning should not be overlooked. One cell of M. ameri*canus* was closed with only three spiders, an egg, and considerable empty space. Although I observed final closure of this nest the female or another wasp was collected with prey near the nest entrance minutes later. The final closure I observed may have been an extensive, several-minute-long temporary closure. A filled nest of M. slossonae barberi was excavated and contained five prey and an egg; shortly thereafter a female with prey arrived and attempted to enter this nest. Whether these observations are, in fact, variations of progressive provisioning behavior or misinterpretations of observations are unknown but they are certainly worth noting.

The behavioral observations presented herein substantiate Bohart and Menke's (1976) inclusion of the former genus *Nitelopterus* as a subgenus of *Miscophus*. My data reveal striking similarities among species in the subgenera *Miscophus* and *Nitelopterus* in nest-site selection, burrow construction, orientation, mechanisms of prey transport, final closure, nest architecture, prey size and their placement in the cell and position of egg attachment. Noteworthy behavioral differences between species in these subgenera include nesting microhabitat and related manner of prey transport, temporary closure activity and kinds (families) of prey. The latter are rather minor distinctions which are ecologically related. Similar differences can be found among species belonging to many genera, e.g., *Tachysphex*, *Ammophila* (Evans, 1959, 1965) and *Bembix* (Evans, 1957, 1966; Evans and Matthews, 1973, 1975).

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### LITERATURE CITED

- Bohart, R. M. and A. S. Menke. 1976. Sphecid wasps of the world. A generic revision. Univ. Calif. Press, Berkeley. 695 pp.
- Cazier, M. A. and M. A. Mortenson. 1965. Studies on the bionomics of sphecoid wasps. IV. Nitelopterus laticeps and Nitelopterus texanus (Hymenoptera: Sphecidae). Pan-Pac. Entomol. 41: 21–29.
- Evans, H. E. 1957. Studies on the comparative ethology of digger wasps of the genus *Bembix*. Comstock Publ. Assoc., Ithaca, N.Y. 248 pp.

—. 1963. Notes on the prey and nesting behavior of some solitary wasps of Jackson Hole, Wyoming. Entomol. News 74: 233–239.

- ———. 1965. Simultaneous care of more than one nest by Ammophila azteca Cameron (Hymenoptera, Sphecidae). Psyche (Camb. Mass.) 72: 8–23.
  - —. 1966. The comparative ethology and evolution of the sand wasps. Harvard Univ. Press, Cambridge, Mass. 526 pp.
- . 1970. Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. Bull. Mus. Comp. Zool. 140: 451–511.
- Evans, H. E. and R. W. Matthews. 1973. Systematics and nesting behavior of Australian Bembix sand wasps (Hymenoptera, Sphecidae). Mem. Am. Entomol. Soc. 20: 1–387.
  . 1975. The sand wasps of Australia. Sci. Am. 233: 108–115.
- Krombein, K. V. 1964. Results of the Archbold Expeditions. No. 87. Biological notes on some Floridian wasps. Am. Mus. Novit. 2201: 1–27.
- 1979. Larridae, pp. 1617–1650. In Krombein, K. V. et al., eds., Catalog of Hymenoptera in America North of Mexico, Vol. 2. Smithsonian Institution Press, Washington, D.C.
- Krombein, K. V. and H. E. Evans. 1954. A list of the wasps collected in Florida, March 29 to April 5, 1953, with biological annotations (Hymenoptera, Aculeata). Proc. Entomol. Soc. Wash. 56: 225–236.
- 1955. Annotated list of the wasps collected in Florida, March 20 to April 3, 1954 (Hymenoptera, Aculeata). Proc. Entomol. Soc. Wash. 57: 223–235.
- Krombein, K. V. and F. E. Kurczewski. 1963. Biological notes on three Floridian wasps (Hymenoptera: Sphecidae). Proc. Biol. Soc. Wash. 76: 139–152.
- Kurczewski, F. E. 1969. Comparative ethology of female digger wasps in the genera *Miscophus* and *Nitelopterus* (Hymenoptera: Sphecidae, Larrinae). J. Kans. Entomol. Soc. 42: 470–509.